ZooKeys 48: 39–59 (2010)
doi: 10.3897/zookeys.48.446
www.pensoftonline.net/zookeys

RESEARCH ARTICLE

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New genus of diminutive microhylid frogs from Papua New Guinea

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Academic editor: *Franco Andreone* | Received 12 March 2010 | Accepted 31 May 2010 | Published 09 June 2010

urn:lsid:zoobank.org:pub:4963BDFF-0A2D-4005-AC8D-5ACCA7FAC38A

Citation: Kraus F (2010) New genus of diminutive microhylid frogs from Papua New Guinea. ZooKeys 48: 39–59. doi: 10.3897/zookeys.48.446.

Abstract

A new genus of diminutive (10.1–11.3 mm) microhylid frogs is described from New Guinea that is unique in its combination of having only seven presacral vertebrae, a reduced phalangeal formula that leaves the first fingers and first toes as vestigial nubs, and reduction of the prepollex and prehallux to single elements. Relationships to other genera are unknown, but overall similarity suggests some relationship to *Cophixalus*, although that genus also differs in some muscle characters and likely remains paraphyletic. The new genus contains two species, which are among the smallest known frogs in the world. Their miniaturization may be related to their inhabiting leaf litter, exploitation of which may select for small size. The new genus is currently known only from one mountaintop in the southeasternmost portion of New Guinea and another on a nearby island. This region is part of the East Papuan Composite Terrane and, should this lineage prove endemic to that region, it may suggest that it originated prior to that geological unit's docking with mainland New Guinea at 23–29 MY.

Keywords

ecomorph, Microhylidae, Milne Bay Province, miniaturization, *Paedophryne* gen. n., smallest frogs

Introduction

The Asterophryinae is one of 11 subfamilies of microhylid frogs, but it contains more than half the species diversity within that family (Frost 2010). This subfamily is largely endemic to the Papuan region (comprising New Guinea and satellite islands, the Ad-

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miralty and Bismarck Archipelagos, and the Solomon Islands), contains 250+ species, is monophyletic (Savage 1973, van Bocxlaer et al. 2006, Frost et al. 2006, Roelants et al. 2007, van der Meijden et al. 2007), and is relatively young: molecular evidence suggests the extant members of this clade arose within the past ~30 MY (van Bocxlaer et al. 2006, Roelants et al. 2007), approximately consistent with geological evidence for the origin of New Guinea (Davies et al. 1996, 1997). Taxonomy within Asterophryinae has been fluid, and the number of recognized genera has expanded from nine in the monograph of Parker (1934) to 20 at present (Günther 2009a, Frost 2010), mostly due to partitioning of recognized genera into more tractable, morphologically cohesive (e.g., Zweifel 2000) or monophyletic (Günther 2009a) groups. Nonetheless, additional partitioning is necessary to achieve a completely monophyletic taxonomy of Asterophryinae (Köhler and Günther 2008), and species diversity within this clade, though great, is severely underestimated (FK, unpubl. data).

Asterophryinae is morphologically and ecologically diverse, encompassing a variety of fossorial, terrestrial, semi-aquatic, scansorial, and arboreal forms (Burton 1986, Menzies 2006, FK, unpubl. data). This range of ecological diversity is greater than that for any other microhylid clade, and is rare within amphibian families generally. Furthermore, many of these adaptive ecotypes have clearly been derived independently, appearing in otherwise unrelated asterophryine lineages (Köhler and Günther 2008). However, the exact number of independent origins of each ecotype has yet to be determined, and our understanding of asterophryine morphological diversity continues to expand and evolve.

During the course of conducting biotic surveys in Papua New Guinea I discovered two new species of a diminutive, morphologically unique asterophryine frog that expand the ecomorphological range already known for the subfamily. Closer examination indicates that these species represent a lineage showing a combination of osteological and myological attributes that do not allow them to be accomodated within any existing genus. I take this opportunity to place these frogs in a new genus and describe the constituent species.

Materials and methods

All measurements were made with digital calipers or an optical micrometer to the nearest 0.1 mm, with the exception that disc widths were measured to the nearest 0.01 mm. Measurements, terminology, and abbreviations follow Zweifel (1985) and Kraus and Allison (2006): body length from snout–vent (SV); tibia length from heel to outer surface of flexed knee (TL); horizontal diameter of eye (EY); distance from anterior corner of eye to center of naris (EN); internarial distance, between centers of external nares (IN); distance from anterior corner of eye to tip of snout (SN); head width at widest point, typically at the level of the tympana (HW); head length, from tip of snout to posterior margin of tympanum (HL); horizontal tympanum diameter (TY); width of the third finger disc (3^{rd} F); and width of the fourth toe disc (4^{th} T).

I confirmed skeletal and musculature features by dissection, X-ray, and double clearing and staining of select specimens; I follow the terminology of Fabrezi and Alberch (1996) for the carpals. Type specimens are deposited in the Bernice P. Bishop Museum, Honolulu (BPBM). All latitude and longitude coordinates use the Australian Geodetic Datum, 1966 (AGD 66).

Genus *Paedophryne* Kraus, gen. n.

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Type species. *Paedophryne kathismaphlox* sp. n.

Content. Two species: *Paedophryne kathismaphlox* sp. n., and *P. oyatabu* sp. n.

Diagnosis. A genus of minute (male SV = 10.1 mm, female SV = 10.4–11.3 mm) frogs with short legs (TL/SV = 0.35–0.40); eleutherognathine jaw; absence of clavicles, procoracoid cartilage, and omosternum (Fig. 1A); seven presacral vertebrae lacking neural crests (Fig. 2B); tips of digits flattened; phalangeal formula 1-2-3-2 on hand, 1-2-3-4-2 on foot, reducing digits F1 and T1 to vestigial nubs (Fig. 1C, D); prepollex and prehallux each reduced to a single element; *M. depressor mandibulae* overlying posterior margin of tympanum (Fig. 3G); *M. adductor mandibularis anterior longus* small and inserting only on lateral portions of frontoparietals (Fig. 3H); *M. submentalis* hypertrophied (Fig. 3I); and tongue long, straplike, attached to floor of mouth along anterior third.

Comparisons with other genera. The new genus differs from all known genera within the Asterophryinae in having the phalanges on the first digits of each hand and foot reduced to tiny cartilaginous elements, imparting to these digits the external appearance of a rudimentary nub (Fig. 4D, E, 5D, E), and in having the prepollex and prehallux reduced to single elements. Its diminutive size also distinguishes it from the vast majority of other asterophryines: although a few small species of *Albericus*, *Aphantophryne*, *Choerophryne*, *Cophixalus*, and *Oreophryne* approach this small a size, only one species of *Oreophryne* attains it. *Paedophryne* further differs from all other asterophryine genera except *Aphantophryne*, some *Albericus* (Menzies 1997), and occasional aberrant individuals of *Cophixalus* (Zweifel & Parker 1989) in having seven (instead of eight) presacral vertebrae; and the length and narrowness of the straplike tongue is only approximated in some other very small species of *Cophixalus* and some *Oreophryne*.

The small species of *Albericus*, *Choerophryne*, and *Oreophryne* are most readily distinguished from *Paedophryne* by having expanded digital discs; as well, the last-named retains clavicles and a procoracoid cartilage. The new genus is superficially most similar to *Aphantophryne* (in vertebral number, short legs, and having the *M. depressor mandibulae* overlying the posterior margin of tympanum, Fig. 3G) and to smaller species of *Cophixalus* (in general appearance and tendency toward digital reduction in some species). In addition to the characters noted above, *Paedophryne* differs from *Aphantophryne* in its more gracile habitus (squat in *Aphantophryne*); in having the tips

of the digits flattened (rounded in *Aphantophryne*); in having a long, straplike tongue (ovoid in *Aphantophryne*); in its more widely expanded sacral diapophyses; in lacking neural crests on the presacral vertebrae (present in *Aphantophryne*); and in having the *M. adductor mandibularis anterior longus* small and inserting only on lateral portions of frontoparietals (*M. adductor mandibularis anterior longus* hypertrophied and inserting on the medial portions of frontoparietals in *Aphantophryne*, Fig. 3B, Table 1). *Paedophryne* further differs from all *Cophixalus* species in lacking neural crests on the presacral vertebrae (present in *Cophixalus*), differs from all *Cophixalus* species except *C. sphagnicola* Zweifel & Allison in having the *M. submentalis* hypertrophied (*M. submentalis* a small strap in *Cophixalus*, Fig. 3C), and differs from all *Cophixalus* except *C. cryptotympanum* Zweifel and *C. kaindiensis* Zweifel in having the *M. depressor mandibulae* overlying the posterior margin of the tympanum (*M. depressor mandibulae* runs entirely behind posterior margin of tympanum in all other *Cophixalus*, Fig. 3D, Table 1).

Distribution. Known from one mountain in the southeastern tip of New Guinea and from one mountain on nearby Fergusson Island, D'Entrecasteaux Islands (Fig. 6).

Etymology. The name is a feminine, latinized noun derived from the Greek "paidos", meaning "child", and "phryne", meaning "toad". It refers to the juvenilized appearance of the frogs.

***Paedophryne kathismaphlox* sp. n.**
urn:lsid:zoobank.org:act:3B527D14-119D-4190-8A76-0FAD5D3A0B7D
Figs 1, 2, 3G, H, I, 5, 7

Holotype. BPBM 17977 (field tag FK 7471), adult female, collected by local villagers on NE slope Mt. Simpson, 10.03157°S, 149.57667, 2170 m, Milne Bay Province, Papua New Guinea, 21 February 2003.

Paratypes (n = 3). BPBM 17975, 35353, same data as holotype, except collected 19 February 2003; BPBM 17976, same data as holotype.

Diagnosis. A minute microhylid (male SV = 10.1 mm, female SV = 10.4–10.9 mm) with the features of the genus and a relatively short leg (TL/SV = 0.35–0.39, Fig. 4A); short snout (EN/SV = 0.067–0.079, EN/IN = 0.78–0.80, Fig. 4C); medium-sized eye (EY/SV = 0.12, EY/SN = 0.92–1.00, Fig. 4C); dorsal pattern of small dark-brown blotches on a dark-brown ground (Fig. 4A); ventral pattern of tiny, scattered light straw flecks on a dark-brown ground (fig 4B); and a burnt-orange patch (in life) below the anus that contrasts with the dark-brown on the remainder of the animal.

Comparisons with other species. The new species differs from other asterophryines in the characters that typify the genus and in its unique burnt-orange rump patch.

Description of holotype. An adult female with a small mid-ventral incision. Head moderately wide (HW/SV = 0.35, Fig. 4A), with steeply oblique loreal region; canthus rostralis rounded, slightly convex when viewed from above; nostrils directed anterolaterally, closer to tip of snout than to eyes; internarial distance larger than distance from

Table 1. Features diagnosing *Paedophryne* gen. n. from its most similar-appearing relatives. Features given for *Cophixalus* exclude mention of uncommon variants discussed in the text.

Character	*Aphantophryne*	*Cophixalus*	*Paedophryne*
Number of presacral vertebrae	8	8	7
Neural crests	present	present	absent
Number of elements in prepollex	2	2-3	1
Number of elements in prehallux	2	2-3	1
Phalangeal formula on hand	2-2-3-3	usually 2-2-3-3, sometimes 1-2-4-2, 2-2-4-2, or 2-2-3-4	1-2-3-2
Phalangeal formula on foot	2-2-3-4-3	2-2-3-4-3 or 2-2-3-4-2	1-2-3-4-1
Tongue	Ovoid	Usually ovoid; straplike in some small species	Long, straplike
M. adductor mandibularis anterior longus	hypertrophied; inserts on medial portions of parietals	small; inserts on lateral portions of parietals	small; inserts on lateral portions of parietals
M. depressor mandibulae	overlies posterior margin of tympanum	entirely behind posterior margin of tympanum	overlies posterior margin of tympanum
M. submentalis	hypertrophied	small straps	hypertrophied

naris to eye (EN/IN = 0.80, IN/SV = 0.095, EN/SV = 0.076); snout rounded when viewed from the side or from above (Fig. 4A, C); eyes moderately large (EY/SV = 0.12; EY/SN = 0.93, Fig. 4C), pupil horizontal; eyelid more than half width of interorbital distance; tympanum indistinct and small (TY/SV = 0.057), visible only when skin dries slightly. Skin smooth; supratympanic fold absent. Fingers unwebbed, flattened; F1 very reduced in size; relative lengths 3>2=4>1 (Fig. 4D). Disc present only on F3, not wider than penultimate phalanx, circum-marginal groove absent. Subarticular and metacarpal tubercles absent. Toes unwebbed; T2, T3, and T4 with flattened discs, but only T4 has a terminal groove. Fifth toe reduced in size, with round tip and no disc; T1 a vestigial nub; relative lengths of toes 4>3>2=5>1 (Fig. 4E). Toe discs barely wider than finger disc ($3^{rd}F/4^{th}T$ = 0.85); disc of fourth toe not wider than penultimate phalanx. Subarticular and metatarsal tubercles absent. Hind legs rather short (TL/SV = 0.39, Fig. 4A). Tongue elongate, straplike, anterior third attached to floor of mouth.

In preservative, dorsum medium brown, irregularly and vaguely marked with darker brown, but pattern indistinct (Fig. 4A); darker markings somewhat more obvious on limbs. Face and behind eye brown spotted with light straw brown (Fig. 4C). Venter and under legs dark brown with scattered light straw-brown flecks; rear of thighs same (Fig. 4B). Dirty gray-white patch below anus and proximal portion of thighs (Fig. 4B). Iris black.

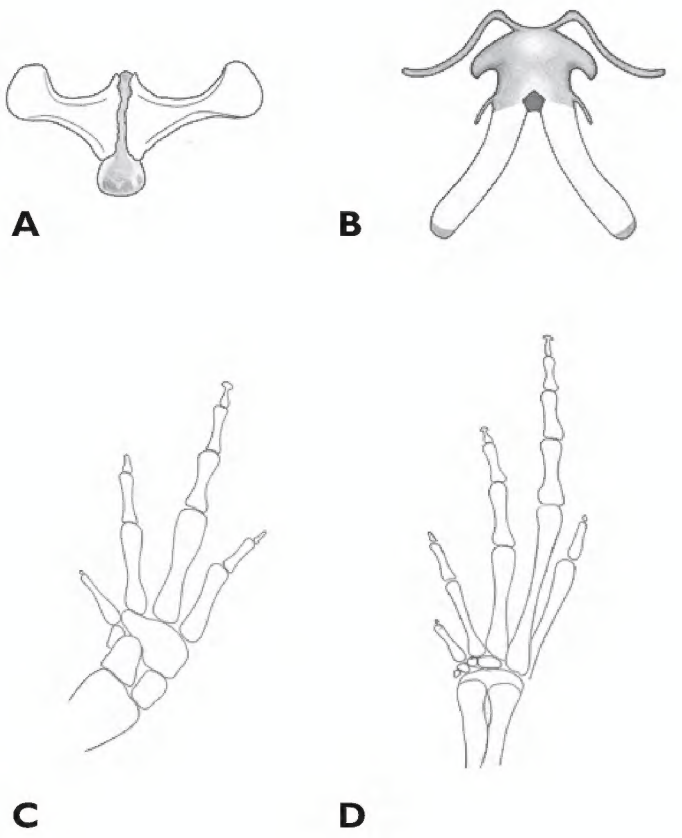

Figure 1. A Pectoral girdle **B** hyoid **C** ventral view of bones of right hand, and **D** dorsal view of bones of right foot of *Paedophryne kathismaphlox* (BPBM 35353).

Measurements (in mm): SV = 10.5, TL = 4.1, HW = 3.7, HL = 3.3, IN = 1.0, EN = 0.8, SN = 1.4, EY = 1.3, TY = 0.6, 3rd F = 0.33, 4th T = 0.39.

Variation. There is little mensural variation in the small type series (Table 2); the same is true for color pattern. The holotype is marginally lighter in ground color than the three paratypes; two paratypes have a vague, lighter brown interorbital bar; and the light ventral flecks in the type series vary from minute to small in size. The skin of the three paratypes is more rugose than seen in the holotype, with each animal appearing rather warty in preservative. Each of these three also clearly had warty or rugose skin in life (Fig. 7).

Osteology. Frontoparietals narrower anteriorly than posteriorly; separate anteriorly, fused posteriorly and fused to exoccipital. Prootics inflated, lacking dorsal crest (Fig. 2A). Sphenethmoid ossified posteroventrally and dorsally, but chondrified anteroventrally. Nasals large but barely meeting at midline, with posterior ramus, chondrified peripherally, hollow centrally, overlying dorsal portion of sphenethmoid (Fig. 2A). Squamosal ossified centrally, chondrified distally, articulating on anteroventral/anterolateral surface of prootic. Quadratojugal largely chondrified. Columella large, ossified centrally, chondrified distally, surrounded by chondrified tympanic annulus. Maxilla largely chondrified centrally, including palatine process. Dorsal process of premaxilla well ossified, slender relative to width of labial process; labial process poorly mineralized. Vomers two large chondrified plates meeting at midline, without teeth or lateral processes. Mentomeckelians chondrified at both ends, connected to dentary by hinge, connected to each other by thin strap of cartilage.

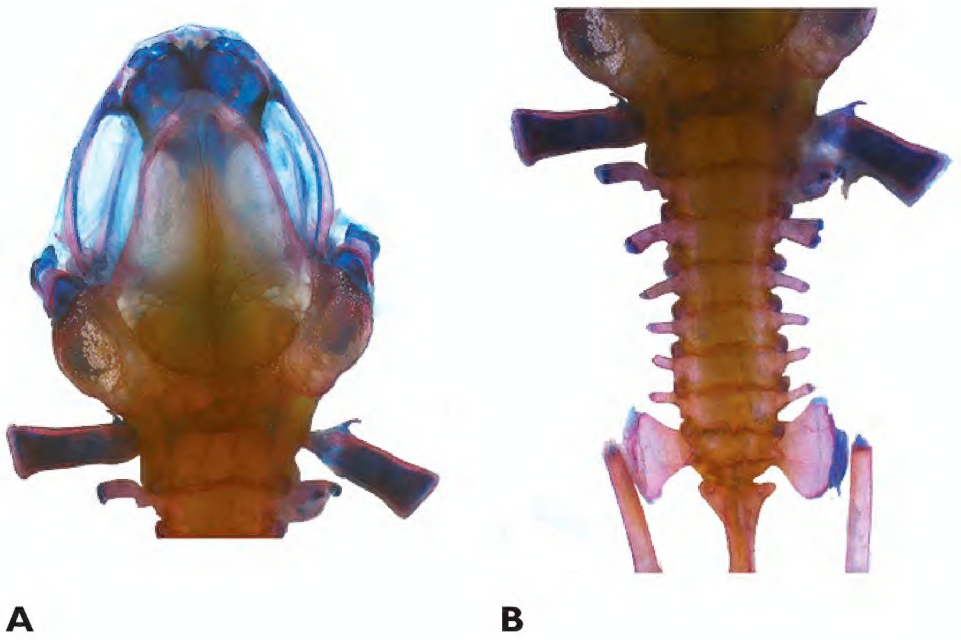

Figure 2. Photos of **A** skull, and **B** vertebral column of *Paedophryne kathismaphlox* (BPBM 35353).

Scapulae, suprascapulae, and coracoids present; first two fully ossified; suprascapula largely chondrified centrally, ossified peripherally, with small anterodorsal chondrified hook curving laterally (Fig. 2A). Clavicles, procoracoids, and omosternum absent; sternum a small, poorly chondrified plate (Fig. 1A).

Seven presacral vertebrae relatively stout, with length approximately one-third to one-half width; longer anteriorly, progressively narrowing posteriorly; all but the first with transverse processes, these longer anteriorly, progressively decreasing posteriorly, most with chondrified tips (Fig. 2B). Neural crests absent. Sacrum with widely expanded diapophyses.

Table 2. Mensural data for type series of *Paedophryne kathismaphlox* sp. n.

Character	BPBM 17975	BPBM 17976	BPBM 17977	BPBM 35353
	female	female	female	male
SV (mm)	10.4	10.9	10.5	10.1
TL/SV	0.35	0.38	0.39	0.39
EN/SV	0.067	0.073	0.076	0.079
IN/SV	0.087	0.092	0.095	0.099
SN/SV	0.13	0.12	0.13	0.12
TY/SV	0.058	0.073	0.057	0.050
EY/SV	0.12	0.12	0.12	0.12
HW/SV	0.38	0.35	0.35	0.37
HL/SV	0.28	0.32	0.31	0.31
3^{rd}F/SV	0.024	0.028	0.031	0.029
4^{th}T/SV	0.037	0.032	0.037	0.035
EN/IN	0.78	0.80	0.80	0.80
3^{rd} F/4^{th} T	0.66	0.86	0.85	0.83
HL/HW	0.74	0.92	0.89	0.84
EY/SN	0.92	1.00	0.93	1.00

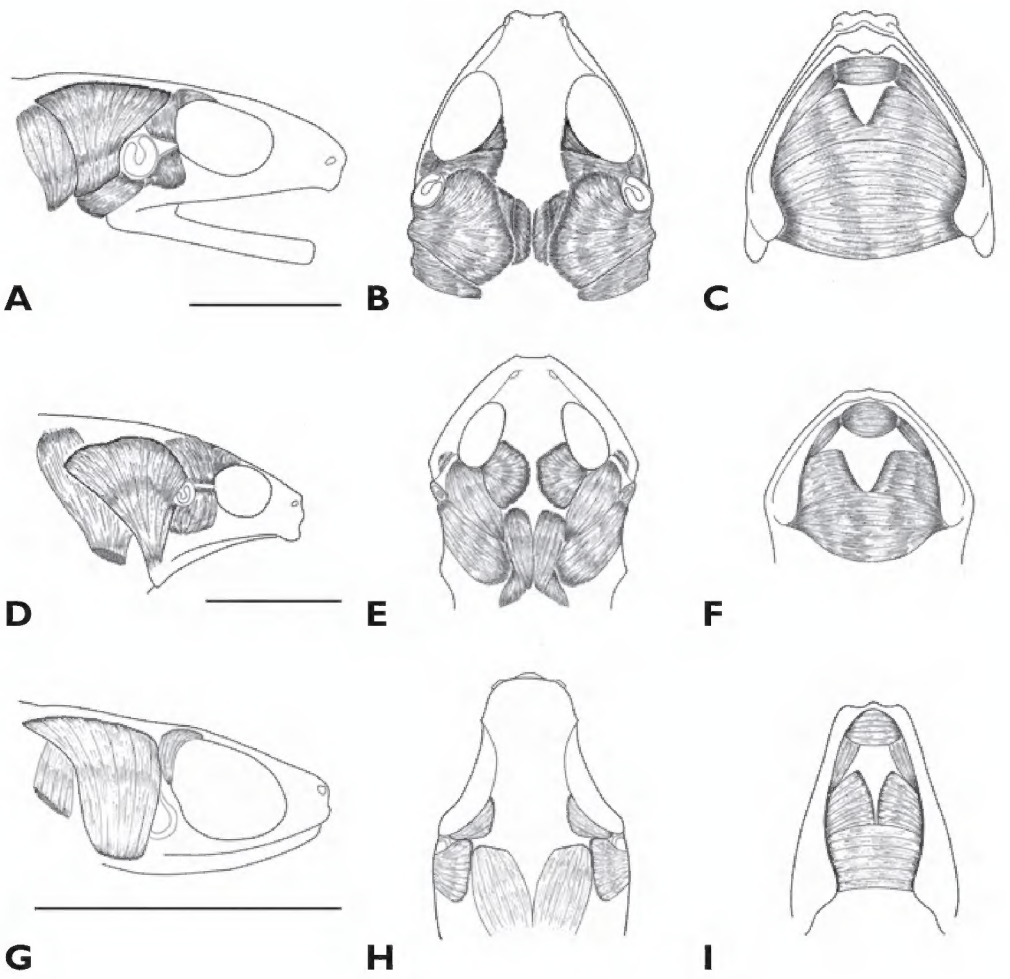

Figure 3. A Lateral **B** dorsal, and **C** ventral superficial head muscles for *Cophixalus verrucosus* (BPBM 15282) **D** lateral **E** dorsal, and **F** ventral superficial head muscles for *Aphantophryne pansa* (BPBM 25278), and **G** lateral **H** dorsal, and **I** ventral superficial head muscles for *Paedophryne kathismaphlox* (BPBM 35353). Scale bar = 5 mm.

Hyoid plate cartilage, with slight mineralization anteromedially and posteriorly, and with recurved anterolateral processes and thinner posterolateral processes; hyales recurved, chondrified; posteromedial processes ossified, elongate, slightly curved, chondrified at distal ends; ventromedial portion of hyoid proximal to the posteromedial processes with a pentagonal thickening (Fig. 1B).

Hand with six carpal elements: small distal carpal 2, distal carpals 3–5 fused into a single large element, prepollex reduced to a single element, and a large radiale lying between a small Element Y and moderate-sized ulnare (Fig. 1C). Metacarpals long and relatively wide; phalanx of F1 unossified, reduced to a vestigial spot of cartilage; two phalanges on F2, three on F3, two on F4 (Fig. 1C). Terminal phalanx of F3 with expanded, T-shaped tip; those of F2 and F4 pointed, unexpanded (Fig. 1C). Foot with four tarsal elements, with prehallux reduced to a single element. Metatarsals long and relatively narrower than metacarpals; phalanx of T1 unossified, reduced to a vestigial spot of cartilage; two phalanges on T2 and T5, three on T3, four on T4 (Fig. 1D). Terminal phalanges of T3 and T4 with expanded, T-shaped tips; that of T2 pointed, unexpanded; those of T1 and T5, vestigial and rounded (Fig. 1D).

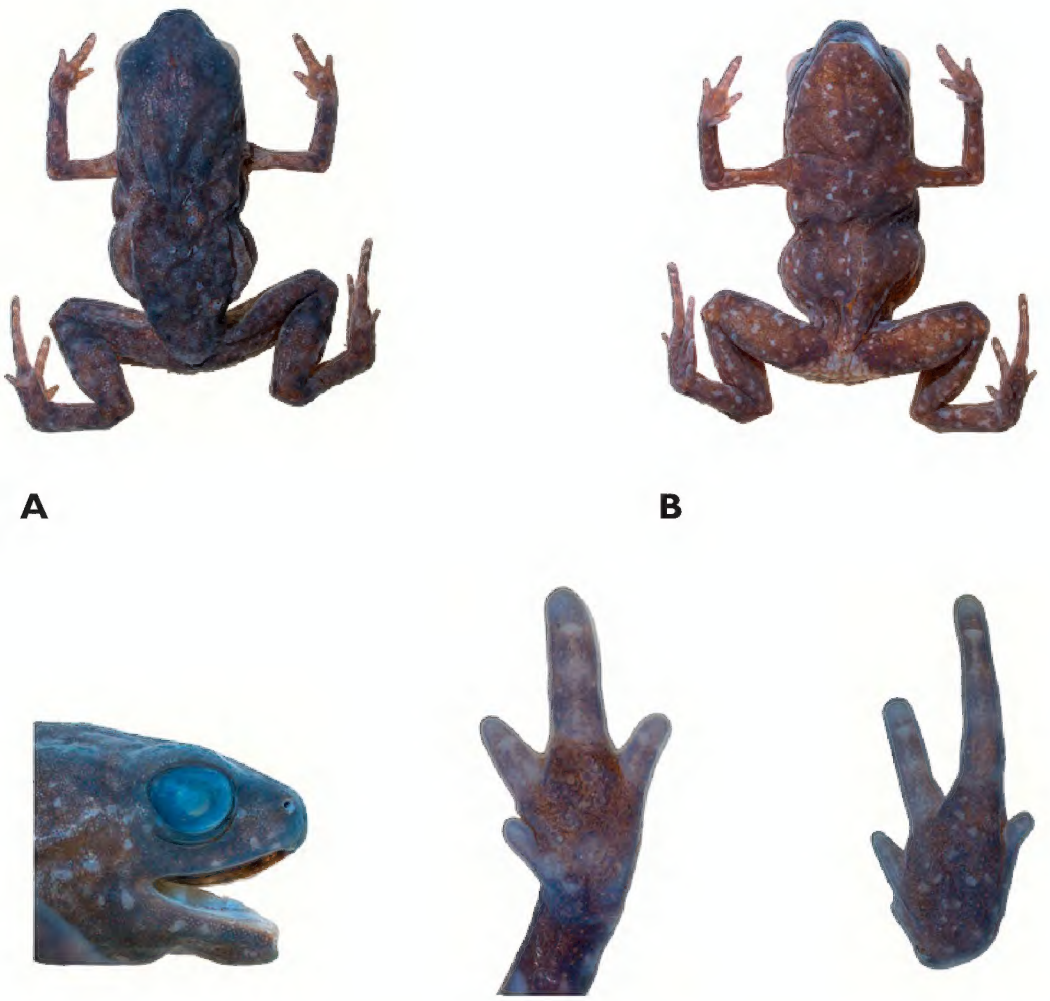

Figure 4. A Dorsum **B** ventrum **C** side of head **D** palmar view of left hand, and **E** plantar view of left foot of holotype of *Paedophryne kathismaphlox* (BPBM 17977).

Color in life. BPBM 17975: "Dorsum brown with irregular black markings; large brown patch on back of thighs near anus. Venter black with gray flecks." BPBM 35353: "Dorsum black with dark brick-orange blotches mid-dorsally, on forearm, and on tibia. Large brick-orange patch on back of thighs near anus. Venter black." BPBM 17976 (Fig. 7): "Dorsum mottled black and dark brown. Venter black with blue-white flecks. Burnt-orange anal patch on rear of thighs. Iris burnt orange." Color images of BPBM 17975–76 in life indicate the sides of each animal were black or very dark brown minutely punctated with light blue-gray flecks (Fig. 7). Each had a narrow reddish rim around the pupil.

Etymology. The name is a noun in apposition derived from the Greek roots "kathisma", meaning "rump", and "phlox", meaning "flame". It alludes to the distinctive burnt-orange patch beneath the anus of living animals.

Range. Known only from the type locality on the N side of Mt. Simpson, Milne Bay Province, Papua New Guinea (Fig. 6, filled circle).

Ecological notes. Animals were collected during the day from wet *Dicranopteris linearis* leaf litter at a former hunting camp cleared from *D. linearis* scrub at an ecotone between montane forest and *D. linearis* shrubland. The area appeared to be a former

landslip. The species was syntopic with *Cophixalus timidus* Kraus & Allison and a small undescribed species of *Oreophryne*.

Paedophryne oyatabu **Kraus, sp. n.**
urn:lsid:zoobank.org:act:480959B5-E002-4E48-85CA-C0307CDF9099
Fig. 5

Holotype. BPBM 16433 (field tag FK 6157), adult female, collected by D. Salepuna on E slope Oya Tabu, 9.4591333, 150.7808666, 1400 m, Fergusson Island, Milne Bay Province, Papua New Guinea, 28 August 2002.

Diagnosis. A minute microhylid (female SV = 11.3 mm) with a relatively short leg (TL/SV = 0.40, Fig. 5A), short snout (EN/SV = 0.062, EN/IN = 0.64, Fig. 5C), medium-sized eye (EY/SV = 0.13, EY/SN = 1.07, Fig. 5C), dorsal pattern of a pair of obscure dark-brown chevrons on a lighter-brown ground (Fig. 5A), and ventral pattern of scattered light-gray spots on a dark-brown ground (Fig. 5B).

Comparisons with other species. The new species differs from *Paedophryne kathismaphlox* in its larger size (females to 10.9 mm in *P. kathismaphlox*), shorter snout (EN/SV = 0.067–0.079, EN/IN = 0.78–0.80 in *P. kathismaphlox*), slightly larger eye

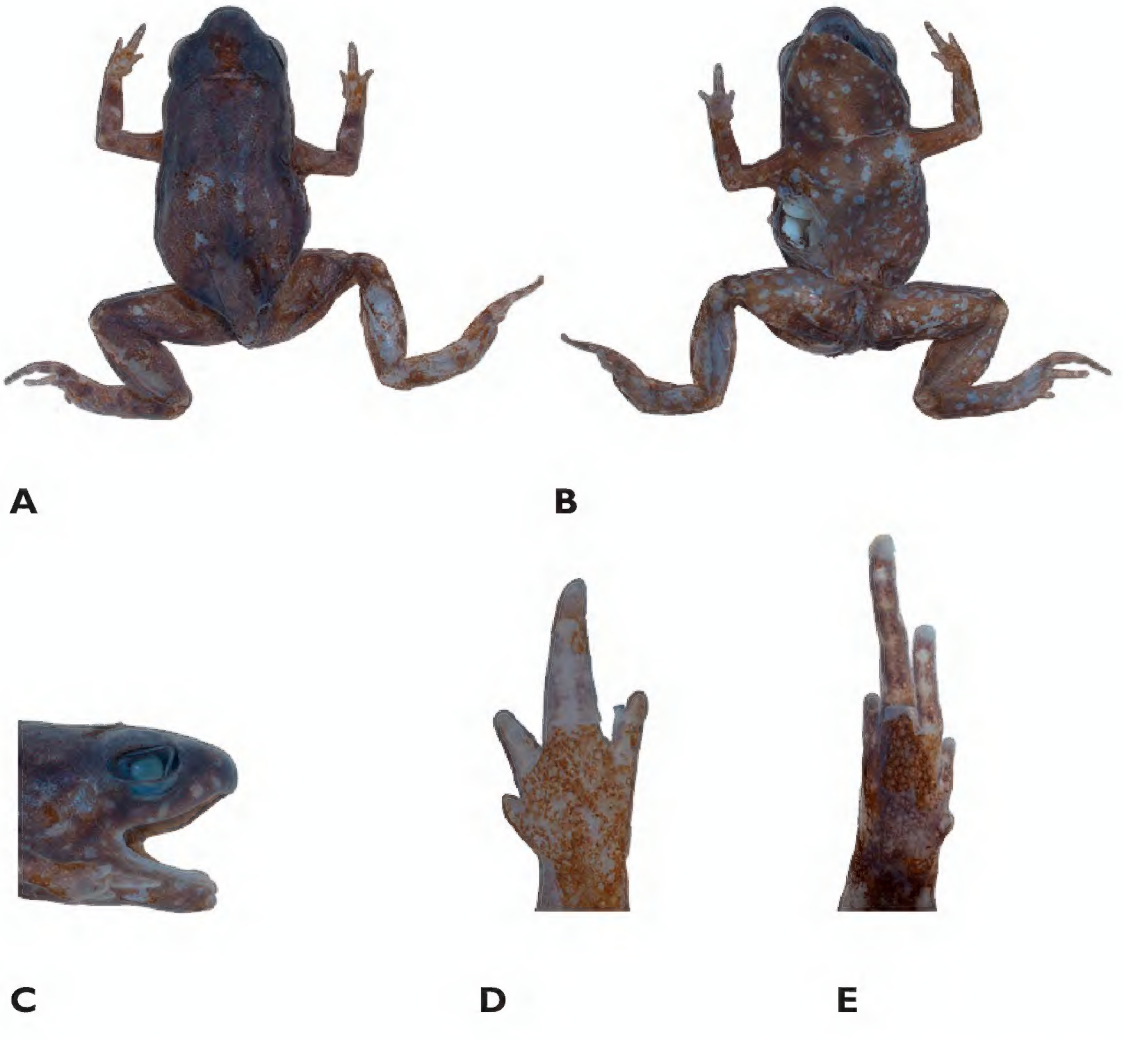

Figure 5. A Dorsum **B** ventrum **C** side of head **D** palmar view of left hand, and **E** plantar view of right foot of holotype of *Paedophryne oyatabu* (BPBM 16433).

(EY/SN = 0.92–1.00 in *P. kathismaphlox*), dorsal pattern of two vague chevrons (vs. irregular small blotches in *P. kathismaphlox*), more boldly spotted venter (light flecks smaller in *P. kathismaphlox*), and absence of a burnt-orange rump patch.

Description of holotype. An adult female with right-lateral incision. Head moderately wide (HW/SV = 0.37, Fig. 5C), with steeply oblique loreal region; canthus rostralis rounded, slightly convex when viewed from above; nostrils directed anterolaterally, closer to tip of snout than to eyes; internarial distance much larger than distance from naris to eye (EN/IN = 0.64, IN/SV = 0.097, EN/SV = 0.062); snout rounded when viewed from the side or from above (Fig. 5A, C); eyes large (EY/SV = 0.13; EY/SN = 1.07, Fig. 5C), pupil horizontal; eyelid almost as wide as interorbital distance; tympanum indistinct posteriorly, small (TY/SV = 0.062). Skin smooth; supratympanic fold absent. Fingers unwebbed, flattened; F1 very reduced in size; relative lengths 3>2=4>1 (Fig. 5D). Disc present only on F3, not wider than penultimate phalanx, circum-marginal groove absent. Subarticular and metacarpal tubercles absent. Toes unwebbed; T2, T3, and T4 bearing slightly flattened discs, with terminal grooves on T3 and T4. Fifth

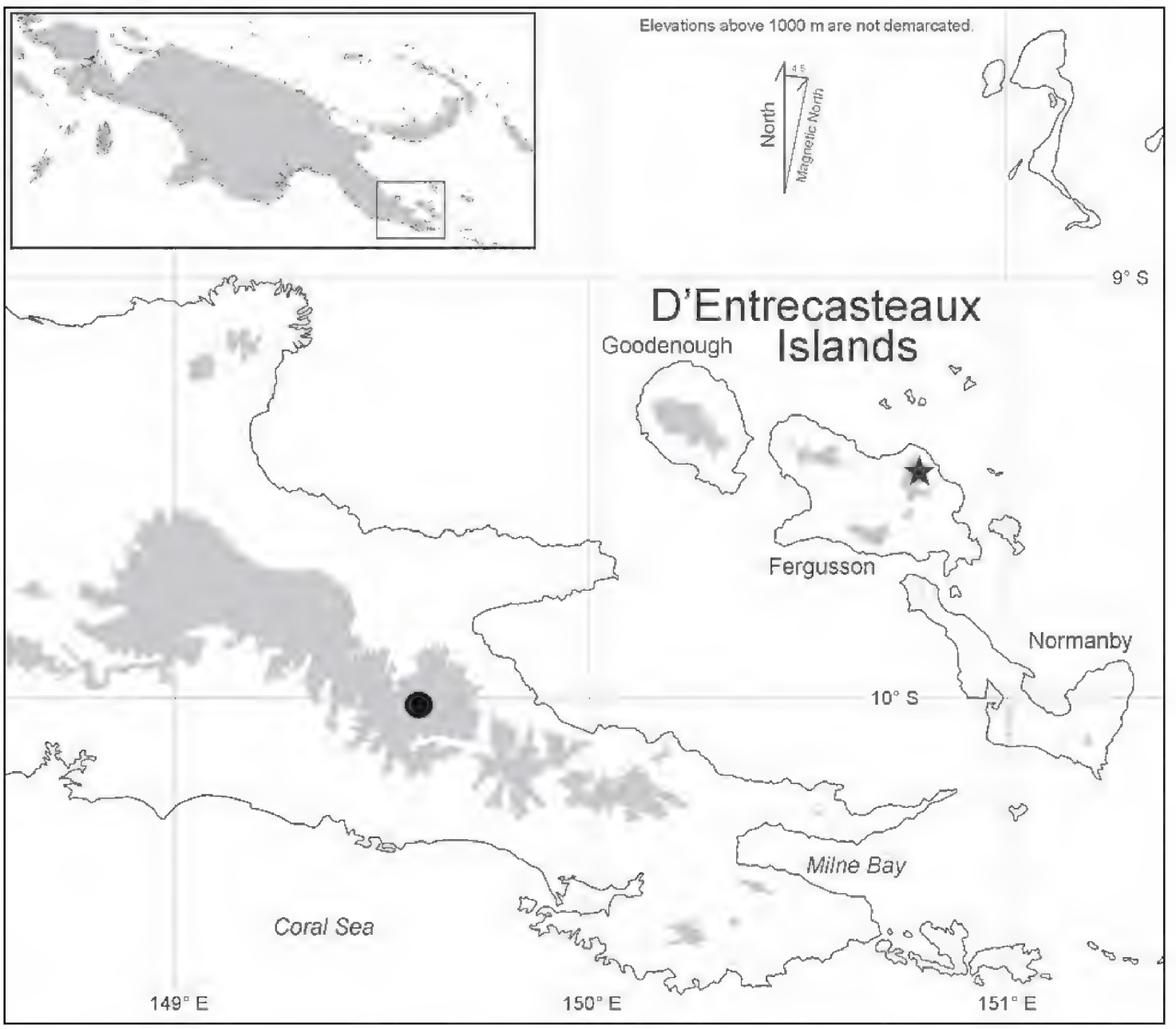

Figure 6. Map of southeastern Papua New Guinea, showing type localities for *Paedophryne kathismaphlox* (filled circle) and *P. oyatabu* (star).

Figure 7. Portrait of paratype of *Paedophryne kathismaphlox* (BPBM 17976) in life.

toe reduced in size, with round tip and no disc; T1 a vestigial nub; relative lengths of toes 4>3>2=5>1 (Fig. 5E). Toe discs somewhat wider than finger disc (3^{rd}F/4^{th}T = 0.80); disc of fourth toe same width as penultimate phalanx. Subarticular tubercles absent; inner metatarsal tubercle small and elongate, outer lacking. Hind legs rather short (TL/SV = 0.40, Fig. 5A). Tongue elongate, straplike, anterior third attached to floor of mouth.

Dorsum brown with obscure, darker brown chevron markings, one in the scapular region, the other in the lumbar region (Fig. 5a). Face and behind eye dark brown with few distinct light-gray spots (Fig. 5C). Venter and under legs dark brown with scattered, moderately large light-gray spots (Fig. 5B). Rear of thighs brown. Iris black.

Measurements (in mm).—SV = 11.3, TL = 4.5, HW = 4.2, HL = 3.6, IN = 1.1, EN = 0.7, SN = 1.4, EY = 1.5, TY = 0.7, 3^{rd} F = 0.28, 4^{th} T = 0.35.

Color in life. "Dorsum light gray brown with two obscure black chevrons on back – one above shoulders, one above groin – and a black mark between the eyes. Forelimbs reddish brown. Entire ventral side black with light-gray flecks."

Etymology. The species is named for its sole known location of occurrence on the highest mountain on Fergusson Island.

Range. Known only from Oya Tabu (Mt. Kilkerran), Milne Bay Province, Papua New Guinea (Fig. 6, star).

Ecological notes. The sole specimen was retrieved by a native collector under a log during the day in mid-elevation (1400 m) montane forest. The area was suffering drought due to an El Niño, so additional frogs or ecological information could not be obtained.

Discussion

The most immediately striking feature of *Paedophryne* is its diminutive size. Lehr and Colima (2008) provided a summary of body sizes seen in what they claimed to be the 40 smallest species of frogs then known. Of these, only two were of smaller average size than *P. kathismaphlox*. Similarly, only five of their listed species may prove smaller than *P. oyatabu*, although the paucity of specimens for this latter species makes comparison less certain. However, Lehr and Colima's (2008) brief review overlooked five species of equally small-sized asterophryines in the genera *Aphantophryne*, *Choerophryne*, *Cophixalus*, and *Oreophryne* (Zweifel and Parker 1989, Richards and Iskandar 2000, Richards and Burton 2003, Kraus and Allison 2006, Richards et al. 2007), and four additional diminutive species in *Austrochaperina*, *Choerophryne* and *Cophixalus* have been described since (Günther 2008, 2009b, Kraus and Allison 2009). Of these nine, only *Oreophryne minuta* Richards & Iskandar is as small as the two *Paedophryne* species, with males of the former ranging from 9.2–11.5 mm SV. All these species, as well as most others mentioned by Lehr and Colima (2008), are diminutive outliers in genera having larger average body sizes. *Paedophryne* may be an exception to this pattern. It clearly constitutes one of the most miniaturized frog clades in the world, yet close relatives of larger size are not apparent (see below).

Aside from overall body size, this new genus expands the range of morphological variation within asterophryine microhylids in two other dimensions. First, it is the only asterophryine to have such an extreme reduction in skeletal elements in the hands and feet. Members of *Aphantophryne*, *Choerophryne*, *Cophixalus*, and *Copiula* examined by me (Appendix I, II) typically have phalangeal formulae of 2-2-3-3 (but may have 1-2-4-2, 2-2-4-2, or 2-2-3-4) for hands and 2-2-3-4-3 or 2-2-3-4-2 for feet, whereas *Paedophryne* has 1-2-3-2 on hands and 1-2-3-4-2 on feet. This marks a net loss of 1–3 phalanges on each hand and 2–4 phalanges on each foot vs. the conditions seen in other small asterophryines. But phalangeal reduction is not limited solely to number: in *Paedophryne* the phalanges that remain on F1 and T1 are vestigial and chondrified, and the second phalanx of T5 is also vestigial (Fig. 1) relative to those seen in other asterophryines. Lastly, all related asterophryines examined by me (Appendix I, II) have the prepollex and prehallux each consisting of two or three elements, whereas *Paedophryne* has only a single element for each, which is uncommon in frogs generally (Fabrezi 2001). Losses in these bony elements produce a unique pattern of reduced digital development that goes considerably beyond what is known in other small asterophryines. This presumably limits the flexibility of the hands and feet and, hence, the degree to which *Paedophryne* species can grasp and climb.

Secondly, seven presacral vertebrae, instead of eight, appear rarely within Asterophryinae, being diagnostic for *Aphantophryne* (Zweifel and Parker 1989) but also present as individual variants in some *Cophixalus* and *Albericus* (Zweifel and Parker 1989, Menzies 1997). The shared state between *Paedophryne* and *Aphantophryne* is likely to have been independently acquired inasmuch as the vertebrae of the two genera differ in other features: *Aphantophryne* has well-developed neural crests while *Paedophryne* lacks them, and the sacral diapophyses are far more expanded in *Paedophryne* than they are in *Aphantophryne*. What, if any, functional consequences attend reduced vertebral number for these frogs remain to be ascertained, but the presence of variation in some other asterophryine species makes the subject liable to direct investigation.

Given the morphological uniqueness exhibited by *Paedophryne* it is not immediately certain wherein its relationships might lie. As noted earlier, it is superficially most similar to several species of small, semi-fossorial or terrestrial species of *Cophixalus* in general appearance and in having indications of digital reduction, such as reduced discs or reduced-sized digits (Kraus and Allison 2000, 2009, Günther 2006). However, this digital reduction in *Cophixalus* is not accompanied by similar loss of bony elements (see, e.g., Günther 2006), and the two genera differ in several other features (Table 1), so it seems unlikely that *Paedophryne* represents merely an extreme form of *Cophixalus.* Further, *Cophixalus* has historically been a dumping ground for asterophryines having an eleutherognatine jaw but lacking clavicles, procoracoid cartilages, and omosternum (Parker 1934). In recent decades, the genera *Albericus*, *Aphantophryne*, and *Copiula* have been removed from this genus (Menzies and Tyler 1977, Zweifel and Parker 1989, Burton and Zweifel 1995), and the morphological diversity still remaining within *Cophixalus* makes its monophyly questionable. Until such monophyly is demonstrated, it is unclear what a "close relationship" between *Paedophryne* and a paraphyletic *Cophixalus* would signify. None of the other asterophryine genera of small size appears particularly similar to *Paedophryne*: *Albericus* is arboreal or scansorial and has expanded digital discs; the scansorial or terrestrial *Choerophryne* has expanded digital discs and a long snout involving horizontal orientation of elongated alary processes of the premaxillae; the terrestrial *Copiula* has expanded digital discs and a serous rostral gland; *Aphantophryne* is squat with rounded digits and exhibits several other differences from *Paedophryne* (Table 1); and *Austrochaperina* and *Oxydactyla* have clavicles, procoracoids, and an omosternum. None seems a likely candidate for sister-taxon to *Paedophryne*, and resolution of this question will require a comprehensive assessment of asterophryine relationships.

What accounts for the extremely small size of *Paedophryne*? As the name suggests, *Paedophryne* has several features that suggest morphological juvenilization, or paedomorphosis. Among these are the loss of bony elements in the hands and feet, chondrification of many of the cranial elements, overall size miniaturization, and reduction in vertebral number. Each of these is suggestive of curtailed development relative to other asterophryines via early truncation of either osteosis or somitogenesis. Of course, to demonstrate whether this is true and which particular heterochronic mechanism might be involved requires interpretation from a resolved cladogram of asterophryine rela-

tionships (Alberch et al. 1979). This is currently lacking, so at present paedomorphosis can only be presumed as likely. Should paedomorphic evolution in *Paedophryne* prove true, as it has for other miniaturized frogs (e.g., Trueb and Alberch 1985, Yeh 2002), similar loss of bony elements in diminutive species of *Cophixalus* and in *Aphantophryne* may reflect independent acquisition in each lineage via paedomorphosis. This may be a consequence of shared lifestyles: each lineage consists of small frogs with relatively short legs and somewhat reduced digits that live in leaf litter and moss. Hence, it may be that exploitation of those constrictive habitats selects for small size and its attendant vertebral, limb, and phalangeal reduction. Based on present evidence, this lifestyle and some of the associated morphological changes were acquired independently within Asterophryinae at least twice (to wit, in *Aphantophryne* and *Cophixalus*, Köhler and Günther 2008), and possible more often. Clarifying this exact number will depend on determining the phylogenetic position of *Paedophryne* and additional miniaturized asterophryines in densely sampled asterophryine phylogenetic investigations.

The biogeographic origins of *Paedophryne* also remain uncertain. New Guinea has been formed over the past 60 million years by the sequential accretion of at least four prior island-arc systems or composite offshore terranes (Pigram and Davies 1987, Davies et al. 1996, 1997). As a result, New Guinea is composed of several dozen geological terranes many with emergent offshore origins and these can be grouped into five major geological regions that reflect different periods of accretion history. Relevant to understanding the history of *Paedophryne* is that the genus is currently known only from the southeastern end of one of these major geological regions: the East Papuan Composite Terrane (EPCT), which comprises the present-day Papuan Peninsula and its immediately adjacent islands. This composite was assembled offshore from a variety of terranes and later sutured *in toto* onto the New Guinea mainland at about 23–29 MY (Davies et al. 1996, 1997). Should additional search prove *Paedophryne* to be restricted to the EPCT, it may suggest that this lineage arose during offshore construction of the EPCT, prior to its docking with the remainder of New Guinea. If true, this could indicate that the Asterophryinae is either older than the estimated date of ~30 MY provided by van Bocxlaer et al. (2006) and Roelants et al. (2007), that *Paedophryne* is one of the earlier lineages of Asterophryinae, or both. Long evolutionary isolation may help explain some of the morphological oddities of the genus as well as present uncertainty about its closest relatives. However, the small size and inconspicuous habits of these frogs have delayed their discovery until the present time, and it may be that the genus is more widespread in New Guinea than currently appreciated. If true, the biogeographic origins of *Paedophryne* would then presumably postdate the origin of the EPCT.

Acknowledgements

I thank David Kizirian and Chris Raxworthy (AMNH) for loan of specimens; Don Cameron for advice on Greek grammar; Carla Kishinami and Pumehana Imada for

specimen processing and documentation; and Shep Myers for preparing the figures. I thank Fred Malesa, Dolasi Salepuna, Jeffrey Tekwae, Brian Uruwa, Dage, Genta Sr., Genta Jr., Munda, Peter, Tanunu, and many other inhabitants of the Bunisi area for field assistance; and Aussiya, Bendo Salepuna, Helen Kurage, Dyson Libai, David Mitchell, Bena Seta and the people of Basima, Bunisi, and Ulua for providing logistical assistance and/or permission to work in the Mt. Simpson and Oyatabu areas. I thank the PNG National Museum and Art Gallery for providing in-country collaborative assistance and the Department of Environment and Conservation, National Research Institute, and Milne Bay Provincial Government for permission to conduct this research. This research was supported by National Science Foundation grants DEB-0103794 and DEB-0743890. This is contribution 2010–009 from the Pacific Biological Survey at the Bishop Museum.

Appendix I

Cleared-and-stained specimens examined for musculature and skeletal attributes

Aphantophryne pansa Fry: Papua New Guinea: Morobe Province: Bulldog Road, 15.5 km. SSW of Wau, 7.477355°S, 146.6757246°E, 2800 m (BPBM 25278, 25286).

Cophixalus balbus Günther: Papua New Guinea: West Sepik Province: 3.2 km SSE Mt. Sapau summit, Torricelli Mts., 550 m (BPBM 22701).

Cophixalus cheesmanae Parker: Papua New Guinea: Morobe Province: 5.3–5.6 km NW summit Mt Shungol, 750–780 m (BPBM 18411).

Cophixalus cryptotympanum Zweifel: Papua New Guinea: Morobe Province, Mt. Kaindi summit, 2360 m (BPBM 9532).

Cophixalus desticans Kraus and Allison: Papua New Guinea: Milne Bay Province: Duabo, Pini Range, 10.4184333°S, 150.3068333°E, 300 m (BPBM 15704, paratype).

Cophixalus iovaorum Kraus and Allison: Papua New Guinea: Central Province: Siruohu, W slope Mt. Obree, 9.44467°S, 148.00923°E, 1560 m (BPBM 19283, paratype).

Cophixalus kaindiensis Zweifel: Papua New Guinea: Morobe Province: Mt. Kaindi summit, 7.3577898°S, 146.6775362°E, 2360 m (BPBM 9529).

Cophixalus parkeri Loveridge: Papua New Guinea: Morobe Province: Biaru Road, 4.2 km N, 4.3 km E of Nako airstrip, 2180 m (BPBM 23724).

Cophixalus pipilans Zweifel: Papua New Guinea: Morobe Province: Kamiali Wildlife Management Area, 500–900 m (BPBM 25738).

Cophixalus riparius Zweifel: Papua New Guinea: Morobe Province: Bulldog Road, 14.5 km SSW of Wau, 7.4682971°S, 146.6793478°E, 2600 m (BPBM 23779).

Cophixalus shellyi Zweifel: Papua New Guinea: Morobe Province: Mt. Missim, 1550–1600 m (BPBM 9364).

Cophixalus sisyphus Kraus and Allison: Papua New Guinea: Central Province: W slope Mt. Obree, 9.4574°S, 148.0277°E, 1760–1870 m (BPBM 19316, paratype).

Cophixalus sphagnicola Zweifel and Allison: Papua New Guinea: Morobe Province: Bulldog Road, 17 km SSW of Wau, 7.4882246°S, 146.6684782°E, 2800 m (BPBM 24334).

Cophixalus timidus Kraus and Allison: Papua New Guinea: Milne Bay Province: vicinity Bunisi, 10.0244565°S, 149.5947176°E, 1420–1540 m (BPBM 18116, paratype).

Cophixalus variabilis Kraus and Allison: Papua New Guinea: Milne Bay Province: near Upaelisafupi Stream, Cloudy Mts., 10.4971°S, 150.2330°E, 715–1000 m (BPBM 15781, paratype).

Cophixalus verrucosus (Boulenger): Papua New Guinea: Milne Bay Province: near Upaelisafupi Stream, Cloudy Mts., 10.4970833°S, 150.2329666°E, 715 m (BPBM 15282).

Paedophryne kathismaphlox Kraus: Papua New Guinea: Milne Bay Province: NE slope Mt. Simpson, 10.03157°S, 149.57667, 2170 m (BPBM 35353, paratype).

Appendix II

X-rayed specimens examined for skeletal attributes

Albericus sanguinopictus Kraus and Allison: Papua New Guinea: Milne Bay Province: Etakaba Creek, N slope of Mt. Simpson, approximately 1 km SE Bunisi Village, 10.0245°S, 149.5947°E, 1490–1540 m (BPBM 17857, paratype)

Aphantophryne pansa Fry: Papua New Guinea: Morobe Province: Bulldog Road, 15.5 km SSW of Wau, 7.477355°S, 146.6757246°E, 2800 m (BPBM 25276).

Aphantophryne sabini Zweifel and Parker: Papua New Guinea: Oro Province: Myola Guest House, 7 km S and 6 km W Mt. Bellamy, 9.1494565°S, 147.7747502°E, 2080 m (BPBM 11562, paratype).

Choerophryne rostellifer (Wandolleck): Papua New Guinea: West Sepik Province: Torricelli Mtns., 1.6 km SSW Mt. Sapau summit, 3.38074°S, 142.51548°E, 1200 m (BPBM 22684).

Cophixalus balbus Günther: Papua New Guinea: West Sepik Province: 3.2 km SSE Mt. Sapau summit, Torricelli Mts., 550 m (BPBM 22693).

Cophixalus desticans Kraus and Allison: Papua New Guinea: Milne Bay Province: Normanby Island, SE end Sewa Bay, 10.0407608°S, 150.9771689°E, 80 m (BPBM 20240, paratype).

Cophixalus interruptus Kraus and Allison: Papua New Guinea: Morobe Province: Oomsis Forestry Camp, 6.6983695°S, 146.8156702°E, 400 m (BPBM 1153, holotype).

Cophixalus iovaorum Kraus and Allison: Papua New Guinea: Central Province: Siruohu, W slope Mt. Obree, 9.44467°S, 148.00923°E, 1560 m (BPBM 19279, paratype).

Cophixalus kaindiensis Zweifel: Papua New Guinea: Morobe Province: Mt. Missim, 7.2404891°S, 146.7961956°E, 2360 m (BPBM 21588).

Cophixalus kethuk Kraus and Allison: Papua New Guinea: Milne Bay Province: Rossel Island, along Rupu River, 11.33537°S, 154.2247°E, 280 m (BPBM 20203, holotype).

Cophixalus linnaeus Kraus and Allison: Papua New Guinea: Morobe Province: Kamiali Wildlife Management Area, 1.3 km N and 6.2 km W of Cape Dinga, 7.295997634°S, 147.092878935°E, 520 m (BPBM 26181, paratype).

Cophixalus melanops Kraus and Allison: Papua New Guinea: Milne Bay Province: Sudest Island, W slope Mt. Rio, 11.5081521°S, 153.4308608°E, 720–800 m (BPBM 20198, holotype).

Cophixalus phaeobalius Kraus and Allison: Papua New Guinea: Morobe Province: Kamiali Wildlife Management Area, 3 km N and 12.9 km W of Cape Dinga, 7.277998011°S, 147.033451568°E, 1520 m (BPBM 26193, holotype).

Cophixalus pipilans Zweifel: Papua New Guinea: Morobe Province: Kamiali Wildlife Management Area, 7. 28188171°S, 147.06502234°E, 900 m (BPBM 25750).

Cophixalus shellyi Zweifel: Papua New Guinea: Madang Province: Adelbert Mts., Mt. Mengam, 4.709692°S, 145.2734234°E, 1500 m (BPBM 5788).

Cophixalus sisyphus Kraus and Allison: Papua New Guinea: Central Province: W slope Mt. Obree, 9.4456521°S, 148.0063578°E, 1580–1640 m (BPBM 19308, paratype).

Cophixalus sphagnicola Zweifel and Allison: Papua New Guinea: Morobe Province: Bulldog Road, 15 km SSW of Wau, 7.477355°S, 146.6757246°E, 2480 m (BPBM 24916).

Cophixalus teztlaffi Günther: Indonesia: Papua Province: E bank Saengga River, 2.4575°S, 133.11082°E, 60–85 m (BPBM 15829).

Cophixalus tagulensis Zweifel: Papua New Guinea: Milne Bay Province: Sudest Island, W slope Mt. Rio, 250–350 m (AMNH 60066, holotype).

Cophixalus timidus Kraus and Allison: Papua New Guinea: Milne Bay Province: N slope Mt. Simpson, 10.03642°S, 149.57488°E, 2480 m (BPBM 18106, paratype).

Cophixalus tomaiodactylus Kraus and Allison: Papua New Guinea: Morobe Province: Kamiali Wildlife Management Area, 2.6 km N and 9.3 km W of Cape Dinga, 7.28188171°S, 147.065022341°E, 900 m (BPBM 26195, paratype).

Cophixalus variabilis Kraus and Allison: Papua New Guinea: Milne Bay Province: near Upaelisafupi Stream, Cloudy Mts., 10.4971°S, 150.2330°E, 715–1000 m (BPBM 15803, paratype).

Cophixalus verecundus Zweifel and Parker: Papua New Guinea: Oro Province: Myola Guest House, 7 km S and 6 km W Mt. Bellamy, 9.1494565°S, 147.7747502°E, 2080 m (AMNH 130410).

Copiula fistulans Menzies and Tyler: Papua New Guinea: Morobe Province: 5.6 km NW summit Mt. Shungol, 6.81625°S, 146.6915333°E, 750 m (BPBM 18633).

Copiula oxyrhina (Boulenger): Papua New Guinea: Milne Bay Province: Misima Island, Oya Tau, 10.65592°S, 152.62765, 860 m (BPBM 17090).

Copiula tyleri Burton: Papua New Guinea: West Sepik Province: Torricelli Mtns., 1.2 km S Mt. Sapau summit, 3.3772645, 142.518018°E, 1120–1320 m (BPBM 22735).

Paedophryne kathismaphlox Kraus: Papua New Guinea: Milne Bay Province: NE slope Mt. Simpson, 10.03157°S, 149.57667, 2170 m (BPBM 17975–77, 35353, type series).

Paedophryne oyatabu Kraus: Papua New Guinea: Milne Bay Province: Fergusson Island, E slope Oya Tabu, 9.4591333, 150.7808666, 1400 m (BPBM 16433, holotype).

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